Improving intercropping: a synthesis of research in agronomy, plant physiology and ecology

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Abstract: Intercropping is a farming practice involving two or more crop species, or genotypes, growing together and coexisting for a time. On the fringes of modern intensive agriculture, intercropping is important in many subsistence or low-input/resource-limited agricultural systems. By allowing genuine yield gains without increased inputs, or greater stability of yield with decreased inputs, intercropping could be one route to delivering 'sustainable intensification'. We discuss how recent knowledge from agronomy, plant physiology and ecology can be combined with the aim of improving intercropping systems. Recent advances in agronomy and plant physiology include better understanding of the mechanisms of interactions between crop genotypes and species – for example, enhanced resource availability through niche complementarity. Ecological advances include better understanding of the context-dependency of interactions, the mechanisms behind disease and pest avoidance, the links between above- and below-ground systems, and the role of microtopographic variation in coexistence. This improved understanding can guide approaches for improving intercropping systems, including breeding crops for intercropping. Although such advances can help to improve intercropping systems, we suggest that other topics also need addressing. These include better assessment of the wider benefits of intercropping in terms of multiple ecosystem services, collaboration with agricultural engineering, and more effective interdisciplinary research.

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Summary

Intercropping is a farming practice involving two or more crop species, or genotypes, growing together and co-existing for a time. On the fringes of modern intensive agriculture, intercropping is important in many subsistence or low-input/resource-limited agricultural systems. By allowing genuine yield gains without increased inputs, or greater stability of yield with decreased inputs, intercropping could be one route to delivering 'sustainable intensification'. We discuss how recent knowledge from agronomy, plant physiology and ecology can be combined with the aim of improving intercropping systems. Recent advances in agronomy and plant physiology include better understanding of the mechanisms of interactions between crop genotypes and species, for example enhanced resource availability through niche complementarity. Ecological advances include better understanding of the context-dependency of interactions, the mechanisms behind disease and pest avoidance, the links between above- and below-ground systems, and the role of micro-topographic variation in coexistence. This improved understanding can guide approaches for improving intercropping systems, including breeding crops for intercropping. Although such advances can help improve intercropping systems, we suggest that other topics also need addressing. These include better assessment of the wider benefits of intercropping in terms of multiple ecosystem services, collaboration with agricultural engineering, and more effective interdisciplinary research.

Keywords

Agriculture, intercropping, organismal interactions, resource use, soil biodiversity, ecosystem services, sustainable intensification

1. Introduction

Intercropping is an ancient practice, placed on the fringes of a 'modern agriculture' dominated by large areas of monocultured, resource-consuming and high-yielding crops (Vandermeer, 2010; Zhang *et al.,* 2010; Li *et al.,* 2013a). However, intercropping may be a means to address some of the major problems associated with modern farming, including moderate yield, pest and pathogen accumulation, soil degradation, and environmental deterioration (Vandermeer, 1989), thereby helping to deliver sustainable and productive agriculture (Lithourgidis *et al.*, 2011).

Intercropping has become a focus for study by a range of agricultural, ecological and environmental scientists with broad research interests (see, for example, Smith *et al.*, 2013; Ehrmann & Ritz, 2014; Li *et al.*, 2014), providing opportunity for inter-disciplinary syntheses combining diverse information on intercropping's potential. This review provides an introduction to intercropping, considers recent insights from agronomy, plant physiology and ecology into the processes and mechanisms underpinning intercropping, and discusses their potential integration to improve intercropping systems. We start by considering the definition, application and potential benefits of intercropping.

Intercropping systems involve two or more crop species or genotypes growing together and co-existing for a time. This latter criterion distinguishes intercropping from mixed monocropping and rotation cropping (Vandermeer, 1989; Li *et al.*, 2013; Fig.1). Intercropping is common particularly in countries with high levels of subsistence agriculture and low levels of agricultural mechanisation. Intercropping is often undertaken by farmers practicing low-input (high labour), low yield farming on small parcels of land (Ngwira *et al.*, 2012). Under these circumstances, intercropping can support increased aggregate yields per unit input, insure against crop failure and market fluctuations, meet food preference and/or

cultural demands, protect and improve soil quality, and increase income (Rusinamhodzi *et al.*, 2012).

In some regions intercropping has been – and remains – the dominant form of agriculture. For example, the area under agro-forestry has been estimated recently to be over a billion ha (Zomer *et al.*, 2009). In Latin America, small-holder farmers grow 70-90% of beans with maize, potatoes, and other crops, whilst maize is intercropped on 60% of the maize-growing areas of the region (Francis 1986). In Africa 98% of cowpeas are intercropped, 90% of beans in Colombia are intercropped; the total percentage of cropped land in the tropics used for intercropping varies from a low of 17% in India to a high of 94% in Malawi (Vandermeer, 1989, and references therein). China contains over 22% of the world's population but has less than 9% of the world arable land. Historically intercropping has contributed greatly to crop production in Chinese agriculture (Tong, 1994).

In Europe, intercropping persists in agroforestry systems such as the Swiss pâturage boisé (wooded grassland systems) and Mediterranean coltura promiscua (cereals and vegetables grown under trees, often olive and fruit trees or vines) (Dupraz & Liagre, 2011). However, it has been lost from many systems: for example, the production area of walnut agroforestry in Italy shrank from 140,000 ha to 10,000 ha between 1960 and 1990 (Eichhorn *et al.*, 2006). It is rare in mainstream agriculture, yet increasing in organic systems (e.g. Hauggaard-Nielsen *et al.,* 2009; Pappa *et al.,* 2011).

Intercrops can be divided into mixed intercropping (simultaneously growing two or more crops with no, or a limited, distinct arrangement), relay intercropping (planting a second crop before the first crop is mature), and strip intercropping (growing two or more crops simultaneously in strips, allowing crop interactions and independent cultivation; Fig.1). Examples of the types and levels of benefits provided by intercropping are

summarised in Supporting Information Table S1. Compared to their component monocrops, they are reported to deliver pest control, similar yields with reduced inputs, pollution mitigation, and greater or more stable aggregate food or forage yields per unit area (Zhu *et al.*, 2000; Lithourgidis *et al.*, 2011; Smith *et al.*, 2013).

Not all intercropping systems provide benefits in terms of all possible metrics. For example in temperate regions grain legumes and cereals intercropped as a forage yield variable gains depending on the cereal and legume species, the sowing ratio, and the specific growing conditions (Anil *et al.*, 1998); legume-cereal mixtures often give lower biomass and protein yields than sole cropped cereals (Table S1). When intercropping benefits do occur, they emerge from more complete exploitation of resources such as solar radiation, water, soil, and fertilisers, from beneficial neighbour interactions (facilitation), and in some cases from continuous soil cover (Table S1; Vandermeer, 1989).

But there are constraints: intercropping may be undesirable when a single standardised product is required, and might lack economies of scale for labour and time management. Intercropping has not usually been seen as suitable for mechanization in an intensive farming system (Feike *et al.*, 2012). Consequently, and despite its potential benefits, intercropping faces huge competition from large-scale, intensive monocrop farming. Thus, to ensure their uptake and enable sustainable agricultural intensification, intercropping systems must be optimised to enhance resource use efficiency and crop yield simultaneously (Li *et al.*, 2013, 2014), while also promoting wider benefits including the delivery of multiple ecosystem services and 'goods' (*sensu* Mace *et al.*, 2012).

A primary challenge for researchers is in understanding the processes and mechanisms underpinning intercropping and the goods it delivers. Such knowledge could allow manipulation of intercropped systems to maximise desired outcomes (e.g. food

production, landscape quality or biodiversity conservation) and thus promote its wider uptake. In the rest of this review we focus on how recent advances in plant physiology, agronomy and ecology might be used to realise enhanced crop yield and quality, and environmental sustainability, i.e. optimising intercropping systems both agronomically and ecologically.

2. Resource Use Efficiency in Intercropping Systems

In 79% of biodiversity experiments biomass production in species-diverse systems was on average 1.7 times higher than in monoculture (Cardinale *et al.*, 2007). Enhanced biodiversity can increase productivity and other ecosystem functions through replacement and complementarity effects. Replacement (or selection) effects result in dominance of mixtures by single, very productive crop species or genotypes: the dominating species increase yields in mixtures relative to expected yields (calculated from monoculture averages of the component species), but not because of beneficial interactions between neighbouring plants (Huston, 1997). Complementarity effects occur when intercropped plants with complementary traits interact positively to increase productivity, and here genuine yield gains are possible (Table S1): both direct facilitation and niche complementarity enable mixtures to yield more than expected from their corresponding monocultures (Trenbath, 1974; Loreau & Hector, 2001; Fig. 2). Here we look in more detail at recent advances in understanding how these mechanisms operate, and then consider how this knowledge can help us design and breed crops specifically for intercropping.

The concept of limiting resources

154 Liebig's "law of the minimum" suggests that crop production is determined by the
155 lack of a single critical resource - the limiting factor. This is common in resource-poor
156 systems, although co-limitation by several factors can occur in optimised agricultural
157 systems (Loomis & Connor, 1992; Zhang *et al.*, 2007). If a cropping system increases the
158 availability of a limiting resource then yield should increase. Common limiting factors are:
159 light, water, oxygen (in waterlogged soils), temperature, or any one of 14 essential mineral
160 elements (Marschner, 2012). In many agricultural systems the limiting factors are nitrogen
161 (N), phosphorus (P), or water availability, whilst cropping season length is often restricted by
162 daylight and temperature extremes. Crop production on 70% of the world's agricultural land
163 can be further restricted by the phytoavailability of iron (Fe), zinc (Zn) and copper (Cu) on
164 alkaline and calcareous soils, or by aluminium (Al) or manganese (Mn) toxicities on acidic
165 soils (White & Greenwood, 2013). Intercropping can increase phytoavailability and
166 acquisition of limiting resources (Table S1), and management of root/rhizosphere
167 interactions can improve resource use efficiency by crops (Zhang *et al.,* 2010; Shen *et al.,*
168 2013; White *et al.,* 2013b; Ehrmann & Ritz *et al.*, 2014; Li *et al.*, 2014; Table S1).
169
170 *Plant traits for resource acquisition and underlying mechanisms*
171 The physiological traits required by crops to maximise resource acquisition are
172 identical in intercropping and monocropping systems, but the challenge of intercropping
173 systems is how best to combine traits of different plants to improve overall performance.
174 Mechanistic studies of intercropping often focus on aboveground plant-plant interactions
175 for light, optimal temperatures and space (Wojtkowski, 2006), but some studies also explore
176 belowground interactions (Zhang *et al.,* 2010; Shen *et al.,* 2013; Li *et al.,* 2014; Ehrmann &

177 Ritz, 2014), including complementary interactions between crop plants and soil biota
178 (Bennett *et al.*, 2013).

179 An example of trait complementarity in tropical intercropping is the 'Three Sisters'
180 polyculture of maize (*Zea mays*), beans (*Phaseolus vulgaris*) and squash (*Cucurbita* spp.;
181 Postma & Lynch, 2012). Squash acts as groundcover during the early season, reducing
182 competition with early-season weeds and water losses by evaporation. Subsequent growth
183 of maize and beans maintains canopy humidity during the later season and maximises the
184 utilisation of light. More generally, in cereal-legume intercrops the shorter, more shaded
185 legume uses captured solar radiation more efficiently in the intercrop than when grown
186 alone (e.g. Kanton & Dennett, 2008; see also examples in Table S1).

187 Where water is the major limitation, intercropping often increases water availability or
188 the efficient use of the available resource (including enhanced water use efficiency, WUE;
189 Morris & Garrity, 1993; Xu *et al.,* 2008), attributed primarily to (1) improved acquisition of
190 water in the soil profile through complementary root distributions (Shackel & Hall, 1984;
191 Mao *et al.*, 2012), (2) hydraulic lift (or hydraulic redistribution) of water by deep rooted
192 crops or mycorrhizal networks (Caldwell *et al.*, 1998; Prieto *et al.*, 2012), and (3) reduced
193 surface runoff (Duivenboden *et al.,* 2000). By analogy with semi-arid savannah communities
194 (which consist of scattered trees or shrubs and an underlying grass/herb layer whose roots
195 occupy different soil niches), water acquisition in intercrops can be improved using crops
196 with complementary root architectures that make most effective use of rainfall (De Barros
197 *et al.*, 2007) and water stored in the soil profile (Zegada-Lizarazu *et al.*, 2006; Fig. 2).
198 Furthermore, there might be potential for the selection of root traits, or mycorrhizal
199 associations, to enhance capture and movement of water to benefit shallow-rooted or non-
200 mycorrhizal plants in arid environments (Burgess, 2011), provided intercropped species are

201 able to effect hydraulic redistribution. It is well established that arbuscular mycorrhizal fungi
202 can improve plant water uptake (Smith & Read, 2008). Hydraulic lift, the passive wetting of
203 drier soil horizons via water movement through roots from wetter horizons, is widely
204 reported (Caldwell *et al.*, 1998). Indeed, Prieto *et al.* (2012) argue that it is "ubiquitous
205 among plants", but there has been little quantification of these effects in intercropping
206 systems. Similarly, and although demonstrated in some semi-arid natural ecosystems
207 (Hortal *et al.,* 2013), the impact of hydraulic lift on nutrient mobilization and nutrient cycling
208 - particularly mediated by increased activity of soil microbial communities near the soil
209 surface - is still underappreciated. Most strategies for improving the use of available water
210 (which could include increasing WUE, for example in irrigated systems) rely on utilising at
211 least one crop with a low water demand: if all crops have high water demands then the
212 opportunities for increasing effective water use through intercropping might be limited,
213 especially in irrigated relay intercropping systems when the ground is sparsely occupied.
214 In intercropping systems with restricted N supply, legumes can increase agricultural
215 productivity (Seran & Brintha, 2010; Altieri *et al.,* 2012). Legumes are pivotal in many
216 intercropping systems (Table S1), and of the top 10 most frequently used intercrop species
217 listed by Hauggaard-Neilsen & Jensen (2005), seven are legumes. Increased N-availability in
218 legume intercrops occurs because (1) competition for soil N from legumes is weaker than
219 from other plants or (2) the non-legumes obtain additional N from that released by legumes
220 into the soil (White *et al.,* 2013b; Li *et al.,* 2013) or via mycorrhizal fungi (van der Heijden &
221 Horton, 2009). Although there may be a general shortage of information on the
222 circumstances under which legume N is transferred to non-legume plants, particularly that
223 N component which is derived from air (Iannetta *et al*., 2013), legumes can contribute up to
224 15% of the N in an intercropped cereal (e.g. Xiao *et al.*, 2004; Li *et al.*, 2009).

225 Crop production on acidic soils is often limited by P availability or Al toxicity (White *et*
226 *al.*, 2013b). Roots of plants adapted to acidic soils, such as peanut, cowpea, potato, sweet
227 potato, maize, beans and brassica, secrete organic acids and phosphatases into the
228 rhizosphere, thereby increasing soil P availability and improving the P-nutrition of
229 beneficiary plants (Fig. 2; Li *et al.,* 2007, 2013; Zhang *et al.,* 2010; Shen *et al.,* 2011; White *et*
230 *al.,* 2013b). The release of organic acids can also protect roots of beneficiary plants from Al-
231 toxicity (Ryan *et al.*, 2011; Simões *et al.*, 2012).

232 Crop production on alkaline and calcareous soils is often limited by the availability of
233 P, Fe, Zn, Mn or Cu (White & Greenwood, 2013; White *et al.*, 2013b) tolerant of mildly
234 alkaline soils, such as brassica, maize, beet and squash, acidify their rhizosphere and secrete
235 organic acids and phosphatases into the soil, thereby increasing P, Fe, Zn, Mn and Cu
236 availability and the mineral nutrition of beneficiary plants (Li *et al.,* 2007, 2013; Zhang *et al.,*
237 2010). In addition, cereals and grasses that release phytosiderophores can improve the
238 acquisition of cationic micronutrients, such as Fe, Zn, Mn and Cu, by those intercropped
239 plants that possess the capacity for metal-phytosiderophore uptake (Zhang *et al.,* 2010; Zuo
240 & Zhang 2011; Li *et al.*, 2014).

241 Roots of complementary plant species can also improve soil stability and soil structure
242 (Obalum & Obi, 2010), thereby improving resource acquisition (Hallett & Bengough, 2013).
243 For instance, tap-rooted species can penetrate compacted soil layers to the benefit of
244 fibrous-rooted species (Chen & Weil, 2010). Their success, however, depends on soil
245 conditions, and in some cases soil physical properties are not affected (Fernandes *et al.*,
246 2011). Plants that promote microbial activities that improve soil fertility, or reduce the
247 populations of pathogenic organisms, can also increase yields in polycultures (Bennett *et al.*,
248 2013).

Designing and breeding for intercropping systems

Plant selection and breeding offer two approaches for improving intercropping systems that to date have rarely been considered. The first is selecting crop species and/or cultivar combinations with traits that maximise positive, and minimise negative, interactions. The second is breeding specifically for combinations of desirable traits. Both approaches are promoted through new knowledge concerning the mechanisms underlying intercropping benefits (as detailed above), but also by our increasingly detailed understanding of trait variation within crop germplasm collections.

The ideotype required of a particular crop is likely to differ for monocropping and intercropping. In monocropping, traits in the chosen crop exploit the environment exclusively for that crop, and focus on increasing the availability and acquisition of limiting resources (White *et al.,* 2013a, b). By contrast, traits for a component of an intercrop are those that optimise complementarity or facilitation (Costanzo & Barberi, 2014); traits can be combined from different crops to overcome resource limitations, resource requirements for each crop can be separated temporally, and the cycling of resources can be optimised during the growing season. New approaches to plant breeding are needed for intercropping systems (Hill, 1996; George *et al.*, 2014). Notably, those crops used currently for assessment of the benefits and management of intercropping have often been bred for and trialled in monoculture systems (Li *pers. comm.*). Inevitably, their selection has not evaluated interactions between above- and below-ground architectures of multiple species, or trade-offs provided among nutrient cycling, water redistribution or non-crop biodiversity when several species co-exist. Elite monoculture varieties, when assessed using criteria relevant to

intercropping systems might, therefore, have suboptimal combinations of traits for intercropping.

As a first step to assessing genotypes for intercropping, diverse germplasm of major crops could be trialled in intercropped and monoculture systems to identify traits delivering favourable yield/quality in one or both systems. Breeding companies are starting to do this (e.g. KWS breeding programme for intercropping bean and maize; Schmidt, 2013). Breeding of plants with traits that benefit a companion crop could also be undertaken, for example by selecting for production of volatiles that deter pests. Finally, the complex interactions that drive resource capture and distribution in intercropped systems could be better understood through resource-based modelling to explore how specific traits can be optimised for complementarity (Postma & Lynch, 2012; Trinder *et al.,* 2012).

3. Applying Ecological Knowledge to Intercropping Systems

Ecologically, we can define the processes occurring in intercropping systems as the negative interactions of competition, parasitism and amensalism, and positive interactions of mutualism and complementarity (Odum, 1968). To understand species interactions, ecologists have long studied the ecology of agricultural systems (see e.g. Vandermeer, 2010). In return, principles and concepts from ecological research into species interactions undertaken in diverse natural systems, for example their context-dependency (Brooker *et al.*, 2008; Schöb *et al.*, 2014), offer possibilities for improving intercropping systems.

Relevant concepts and recent advances in ecological research

Much recent interest has surrounded the effect of environmental context on plant-plant interactions (Brooker *et al.,* 2008). Substantial evidence now indicates that under more

severe environmental conditions (e.g. semi-arid, arctic, alpine or heavily-grazed systems) net beneficial (facilitative) interactions are more common, but are outweighed by negative interactions in productive environments (for example mesic grasslands) as plant growth conditions improve (Li *et al.,* 2013; He *et al.,* 2013). This predictable variation in net plant-plant interactions depending on environmental context has become known as the Stress Gradient Hypothesis (SGH; Brooker *et al.* 2008). Based on the ecological concept of the SGH, we might reasonably expect that the net balance of interactions occurring within intercropping systems may also vary depending on the environmental context. This could explain, for example, some of the between-year and between-site variability found in the benefits of intercropping (Table S1), and provide a framework for tailoring intercropping systems to the local environment. Analyses of the results of intercropping trials have not – to our knowledge – explicitly included a search for the type of patterns predicted by the SGH. Based on the approaches adopted by recent meta-analyses for semi-natural and natural systems (e.g. He *et al.* 2013), we suggest that such an analysis would be relatively straightforward for intercropping systems.

Many recent ecological studies have also explored the biodiversity-function relationship in natural and semi-natural systems, examining when genuine benefits (e.g. enhanced levels or stability of productivity) have arisen from combining genotypes or species in more diverse communities (e.g. Cardinale *et al.,* 2012; Cong *et al.*, 2014), and separating net biodiversity effects into the replacement and complementarity effects discussed earlier (see *Plants traits for resource acquisition and underlying mechanisms*). Several long-term biodiversity grassland experiments have shown that the scale of positive diversity-productivity effects can increase over time (Cardinale *et al.*, 2007; Reich *et al.*, 2012). Recent findings indicate that this strengthening relationship is due to positive

ecosystem feedbacks associated with greater storage of soil C and N over time and subsequent enhanced C and N cycling (Reich *et al.*, 2012; Cong *et al.*, 2014). Such studies are enabling us to understand the mechanisms underlying how enhancing the diversity of primary producers (e.g. vascular plants) has consequences for biodiversity and sustainability at a system level (e.g. Naeem & Li 1997; Handa *et al.*, 2014). With respect to intercropping, the results of these studies can help us to focus on a wider suite of response variables when assessing the benefits and improvement of intercropping systems, as well as helping to identify combinations of plant traits that are complementary under a range of different environmental conditions.

The regulation of pests (to include weeds, invertebrate pests and diseases) provides an excellent example of where a better understanding of fundamental ecological processes can have direct benefit for the improvement of intercropping and crop production in general. Globally, pests are estimated to destroy more than 30% of crop yield annually (Oerke, 2006), while declining insect pollinator abundance (Goulson *et al.*, 2008) could limit the productivity of insect-pollinated crops worldwide (Kremen *et al.*, 2002). There are numerous examples of the benefits in intercropping systems that arise because of pest and pollinator regulation (Table S1), but only recently have the mechanisms behind these benefits been understood. For example, by providing a more complex habitat with a greater diversity of resources for beneficial organisms (Potts *et al.*, 2003; Wäckers, 2004), intercropping systems have the potential to reduce the apparency of crop plants to pests (Finch & Collier, 2012) and increase the abundance and diversity of pollinators and natural enemies of crop pests. As an example of the scale of these effects on crop production, a five-fold increase in the density of banana/plantain clusters intercropped with cocoa was associated with a two-fold increase in the abundance of pollinating midges, equating to a

doubling in cocoa pod set (Frimpong *et al.*, 2011). Furthermore, increased natural enemy activity can lead to reductions in crop damage in intercropped systems (Letourneau *et al.*, 2011); a 50-100% increase in predator species richness and abundance relative to herbivorous pests has been detected in apple orchards inter-planted with aromatic herbs (Beizhou *et al.*, 2012).

Disease suppression is also widely found in intercropping systems (Table S1), with 73% of documented studies reporting reduced disease incidence in intercrops compared to crop monocultures, commonly in the range of 30-40% (but up to 80% in some systems; Boudreau *et al.*, 2013). Disease suppression can result from a variety of factors including decreased host plant availability, altered dispersal by rain, wind and vectors, and microclimatic effects on pathogen establishment (Boudreau *et al.*, 2013). However, increased vegetation diversity does not always translate into increased yield, nor improved pollination and biocontrol services (Letourneau *et al.*, 2011; Cardinale *et al.*, 2012). As discussed with respect to the Stress Gradient Hypothesis, understanding this context dependency may be crucial in tailoring intercropping systems to spatial and temporal variation in environmental conditions.

Recent plant-soil organism interaction studies have also highlighted possibilities for improving intercropping systems (Ehrmann & Ritz, 2014). Specific mechanisms, such as the transport of allelochemicals through common mycorrhizal networks (CMNs), with CMNs possibly acting as “superhighways” directly connecting plants below-ground, allow for systemic signalling across plant populations and directed allelochemical delivery to target plants (Barto *et al.*, 2012). Increasing plant diversity helps to maintain soil organism diversity (van der Putten *et al.,* 2013), and increasing soil organism diversity leads to increased plant productivity with, for example, a greater than 50% increase in shoot biomass observed with

368 increasing mycrorrhizal species number (van der Heijden *et al.,* 1998). Experimental studies
369 have indicated that below-ground organisms can increase attraction of herbivore enemies,
370 decrease herbivore fitness, increase pollinator visits, and protect against pathogens (Orrell
371 & Bennett, 2013). Understanding these networks of interactions provides insights into how
372 soil microbial communities might be managed to improve crop production, and also
373 indicates that increased crop diversity – for example that arising in intercrop as opposed to
374 monocrop systems – could play an important role in this management process.
375 Furthermore, recent applications of structural equation modelling to complex ecological
376 networks (Grace, 2006) could be highly relevant to untangling these complex webs of
377 interactions, and distinguishing clearly which processes are related to final changes in
378 system function (including crop production).

379 Finally, although some recent ecological research is perhaps less obviously relevant it
380 might still have important lessons for improving intercropping. For example, studies linking
381 phylogenies and traits to community productivity (e.g. Cadotte *et al.,* 2009) suggest that
382 intercropped species separated by a greater phylogenetic (i.e. evolutionary) distance might
383 have reduced niche overlap and have greater net complementarity effects. Doubling
384 phylogenetic diversity of experimental grassland communities resulted in a biomass
385 increase of *c*. 20%, and was the most influential factor for productivity after the presence of
386 N-fixers, and before factors such as species richness and functional diversity (Cadotte *et al*.,
387 2009). Co-evolution can also influence interactions: communities of bacteria evolved in
388 mixed species communities increased productivity by *c*. 16% compared to those evolved in
389 monoculture (Lawrence *et al.*, 2012). Organismal co-evolution might therefore enhance
390 ecosystem function. The relative strength of such evolutionary effects versus the unique
391 facilitation mechanisms found in some intercrop combinations (such as enhanced Fe or P

392 mobilisation, Table S1) now needs assessing, but again such questions can be assessed
393 through appropriate meta-analyses. For example, as well as considering whether the results
394 of the SGH are supported by data from intercropping studies, do we also see the patterns
395 we would expect if - for example - phylogenetic conservation of the niche is affecting the
396 strength and direction of interactions, e.g. generally stronger interactions in those cases
397 where intercropped species are phylogenetically more distant?

398 We can summarise the relevance to the improvement of intercropping of these recent
399 advances in ecology in a simple schematic diagram (Fig. 3). The challenge now is to integrate
400 this new ecological knowledge into the design and analysis of the results of intercropping
401 studies. Although some of the processes that we have discussed such as the SGH and
402 phylogenetic niche conservatism might be considered general "rules", we know that others
403 can be highly species and environment dependent, for example the nature of the
404 relationships between plants and mycorrhizal fungi or the occurrence of hydraulic lift. In the
405 first instance we should ask whether certain processes can be demonstrated as operating in
406 intercropping systems. If they are, we need to then use our new understanding to design
407 intercropping systems to account for them. Adopting an ecological approach to understand
408 the underlying mechanisms will be central to achieving this goal.

409

410 *Intercrops and microtopography*

411 The above examples consider mainly organismal interactions, but another critical aspect of
412 the environment is its physical structure. Monoculture farming aims at an environment
413 homogenous at the plant scale, for example an even seedbed that encourages uniform
414 germination across a field (Hallett & Bengough, 2013). But small variations in
415 microtopography can have important impacts by creating closely integrated but distinct

niches, which in turn can enable species co-existence in crop systems. Variation of only a few centimetres in elevation creates large differences in drainage characteristics that can predominate over general soil physical attributes to create drier and wetter regions (Schuh *et al.*, 1993). In semi-arid conditions, plants at the base of the depression have access to more water, but might be shaded by plants on a crest (Harris *et al.,* 1994). In very wet conditions relatively drier crests or ridges provide a more suitable environment for non-hydrophytic plants (Rao & Li, 2003), and a greater depth of unsaturated soil with adequate water to avoid plant stress (as on a crest or ridge) may be an advantage to plants needing to form tubers or rhizomes (He *et al.*, 1999; Henriksen *et al*., 2007). Opportunities clearly exist to manage the local variation in microtopography, and hence factors such as soil water status, to suit particular intercropping combinations. Furthermore, as we unpick these relationships we may be able to relate variation in key traits to microtopographic location, and hence better select for such traits when breeding for intercrops.

Lessons from intercropping for ecology

Despite recent advances in ecological understanding there exist substantial knowledge gaps concerning key organismal interactions, including those between parasites and hosts, above- and below-ground communities, and plants and soil organisms (including legacy effects). As well as the proposal we make above for a flow of information from ecology relevant to the improvement of intercropping systems, in return - and as a brief aside - the study of intercropping may have important lessons for our understanding of natural and semi-natural systems. Obvious questions arise as to whether mechanisms and processes underlying enhanced yield per unit area or sustainability in intercrops operate in natural systems. For example, mechanisms that enhance soil mineral availability have been

identified from intercropping systems, but these processes have not been examined in natural or semi-natural systems. A prime example of this is the potential for some species in alkaline soils – through acidification of the rhizosphere – to increase the availability of elements such as P and Fe, and hence the mineral nutrition of neighbouring plants (see *Plant traits for resource acquisition and underlying mechanisms*, above, and Table S1 for this and other examples). To the best of our knowledge this facilitation mechanism has not been explored in natural and semi-natural plant communities, but could readily be operating.

Furthermore, perhaps some of the key challenges in ecological science can be addressed by studying in detail the ecology of intercropping systems. Ecologists have long struggled to understand the processes by which different combinations of plant traits enable species co-existence and regulate ecosystem function. Intercropping studies can tell us much about niche and trait complementarity, how different trait combinations can influence system function and sustainability, and how these effects may vary depending on the environmental context.

4. Future Perspectives for Intercropping Research

Both agronomy and ecology can clearly contribute to the improvement of intercropping systems. They can enhance crop productivity and resource use efficiency whilst decreasing farming's environmental impact, making intercropping a viable approach for 'sustainable intensification', particularly in regions with impoverished soils and economies where measured benefits have been greatest (Rusinamhodzi *et al.*, 2012). But to realise these benefits, major challenges for research remain. Some of them, for example breeding for intercrops, and understanding better the interactions between plants and other organisms in crop systems, have already been discussed. Here we propose briefly some other aspects

of research that we feel could be important for the development of intercropping systems, and their wider uptake.

Systems understanding of intercropping

Many studies have focussed on particular processes rather than on the interactions between the multitude of processes that occur simultaneously in an arable system. Hence, it is difficult to identify limitations to major processes driving variation in yields or other ecosystem services generated by intercrops. However, true systems research is laborious and needs inputs from numerous disciplines to be effective. This review article has brought together concepts from plant physiology, agronomy and ecology. Even wider interdisciplinary research activities could apply a systems-level approach to understanding the processes operating in intercropping systems, and to move beyond the traditional focus on resources to include the roles of above and below-ground interactions of plants with other organisms.

Intercropping and ecosystem services

More studies are needed to explore the potential of intercropping to deliver ecosystem services beyond crop production, including improving soil and water quality, improving landscape, controlling pests, and mitigating climate change. Ecosystem service approaches should emphasise that intercrops could achieve food security with reduced anthropogenic inputs and lower environmental impact. For example, there is now evidence that increased plant (trait) diversity in grasslands is positively correlated with gross C-allocation below-ground, microbial abundance in soil, microbial diversity and soil C-sequestration (De Deyn *et al*., 2008; 2011). Therefore, increased plant diversity in cropping systems has potential to

488 increase soil physical stability and resilience of microbially-mediated nutrient cycling
489 processes (Pérès *et al*., 2013; Gregory *et al*., 2009; Garcia-Pausas & Paterson, 2011).
490 Consideration of the wider suite of services and goods that can be supplied by intercropping
491 could promote its use, but to achieve this we need more (and better) indicators of service
492 delivery. Benefits are commonly assessed using standard metrics such as crop yield or
493 resource use efficiency (Table S1), but they are not often assessed using metrics of soil
494 health or cultural benefits, not least because such metrics are themselves not well
495 developed. What is critical, though, is achieving a balanced picture of the costs and benefits
496 of intercropping and other alternative food production systems.
497
498 *Agricultural engineering and management*
499 The greatest changes in intensive agriculture in the past 20 years have been made
500 possible by developments in engineering. Precision application of nutrients, reduced tillage,
501 and the use of GM herbicide tolerant crops were all led by industry and promoted by clear
502 farm-gate economic benefits. While generally the targets were increased yield and profit,
503 some innovations such as minimum tillage had perceived benefits for soil sustainability
504 (Powlson *et al.,* 2011). However, the concentration of this technology on monoculture has in
505 many regions diminished or negated the original benefits, for example through the rapid
506 evolution of herbicide resistance in weeds caused by a low diversity of cropping practice
507 (Johnson *et al.*, 2009).
508 Could more diverse systems based on intercropping fare better? As yet, only a small
509 proportion of larger-scale intensive farms employ intercropping as a standard practice
510 (Vandermeer, 1989). Mechanisation in intercropping is nevertheless possible (Tisdall &
511 Adam, 1990) and is perhaps best demonstrated in legume-based systems (Iannetta *et al.*,

2013). More generally, the development of new machinery that can till, weed and harvest at small spatial scales and in complex configurations is needed to encourage uptake of intercropping without greater demands for labour (Lithourgidis *et al.*, 2011). More rapid adoption might also be promoted if benefits are assessed by a wider suite of metrics, and via wider "systems thinking" through the enactment of schemes including payment for ecosystem services (Swinton *et al.*, 2007).

5. Concluding remarks

Intercropping systems clearly have potential for increasing the long-term sustainability of food production under low inputs in many parts of the world. Whilst some of the mechanisms by which they deliver benefits are understood, there is considerable potential to improve intercropping systems to gain either greater yield (or other benefits) with the same inputs, or sustained yield with reduced inputs based on new knowledge from both ecology and agronomy, and the interface between the two disciplines.

In the short term, perhaps the most straightforward approach is simply to trial new combinations of crops to exploit beneficial mechanisms that have already been identified, for example new combinations of cereals and legumes (a widespread focus for current research). Rapid improvements are also possible through the development of new agronomic practices, including the mechanisation of intercropping systems and improved nutrient management, but again such efforts can be taken forward using existing knowledge and experimental approaches.

On a longer time scale, increasing resource use efficiency of intercrops through plant breeding is likely to be the most effective option. However, breeding programmes should explicitly consider multiple traits that would benefit mixed cropping and not simply those

traits known to raise the yield of monocrops. These breeding efforts, as well as the development of management practices tailoring intercropping systems to the local environment, can be guided by the new understanding derived from ecological research into organismal interactions.

Perhaps the most distant from immediate implementation are approaches based on more abstract concepts from ecology including phylogenetic distance and co-evolution. However, the apparent scale of these effects in some ecological studies indicates that they should at least be considered as part of the research agenda for improving intercropping systems: are such processes operating in intercropping systems, what are the scale of these effects, and how can we use this knowledge to guide our crop management or breeding practices?

Applying all of these approaches will need a better exchange of information between ecologists, environmental scientists, agronomists, crop scientists, soil scientists, and ultimately social scientists (for example exploring attitudes to uptake, and developing wider cost/benefit analyses) so that the full potential of intercropping as a sustainable farming system can be realised.

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564 **References**

565 **Altieri MA, Funes-Monzote FR, Petersen P. 2012.** Agroecologically efficient agricultural
566 systems for smallholder farmers: contributions to food sovereignty. *Agronomy for*
567 *Sustainable Development* **32**: 1-13.

568 **Anil, L, Park, J, Phipps, RH, Miller, FA. 1998.** Temperate intercropping of cereals for forage:
569 a review of the potential for growth and utilization with particular reference to the UK.
570 *Grass and Forage Science* **53:** 301-307.

571 **Babikova Z, Gilbert L, Bruce TJ, Birkett M, Caulfield JC, Woodcock C, Pickett J, Johnson D.**
572 **2013.** Underground signals carried through common mycelial networks warn neighbouring
573 plants of aphid attack. *Ecology Letters* **16:** 835-643.

574 **Barto EK, Weidenhamer JD, Cipollini D, Rillig MC. 2012.** Fungal superhighways: do common
575 mycorrhizal networks enhance below ground communication? *Trends in Plant Sciences* **17**:
576 633-637.

577 **Beizhou S, Jie Z, Wiggins NL, Yuncong Y, Guangbo T, Xusheng S. 2012.** Intercropping with
578 aromatic plants decreases herbivore abundance, species richness, and shifts arthropod
579 community trophic structure. *Environmental Entomology* **41:** 872-879.

580 **Bennett AE, Daniell TJ, White PJ. 2013.** Benefits of breeding crops for yield response to soil
581 organisms. In: de Bruijn FJ, ed. *Molecular microbial ecology of the rhizosphere. Volume 1*.
582 Hoboken, NJ, USA: Wiley, 17-27.

583 **Boudreau MA. 2013.** Disease in intercropping systems. *Annual Review of Phytopathology*
584 **51:** 499–519.
585 **Brooker RW, Maestre FT, Callaway RM, Lortie CJ, Cavieres LA, Kunstler G, Liancourt P,**
586 **Tielbbörger K, Travis JMJ, Anthelme F *et al.* 2008.** Facilitation in plant communities: the
587 past, the present, and the future. *Journal of Ecology* **96:** 18–34.
588 **Burgess SSO. 2011.** Can hydraulic redistribution put bread on our table? *Plant and Soil* **341:**
589 25-29.
590 **Cadotte MW, Cavender-Bares J, Tilman D, Oakley TH. 2009.** Using phylogenetic, functional
591 and trait diversity to understand patterns of plant community productivity. *PLoS ONE* **4:**
592 e5695
593 **Caldwell MM, Dawson TE, Richards JH. 1998.** Hydraulic lift: consequences of water efflux
594 from the roots of plants. *Oecologia* **113:** 151-161.
595 **Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM,**
596 **Tilman D, Wardle DA *et al.* 2012.** Biodiversity loss and its impact on humanity. *Nature* **486:**
597 59-67.
598 **Cardinale BJ, Wright JP, Cadotte MW, Carroll IT, Hector A, Srivastava DS, Loreau M, Weis**
599 **JJ. 2007.** Impacts of plant diversity on biomass production increase through time because of
600 species complementarity. *Proceedings of the National Academy of Sciences of the United*
601 *States of America* **104**: 18123-18128.
602 **Chen GH, Weil RR. 2010.** Penetration of cover crop roots through compacted soils. *Plant*
603 *and Soil* **331:** 31-43.
604 **Cong W-F, van Ruijven J, Mommer L, De Deyn GB, Berendse F, Hoffland E. 2014.** Plant
605 species richness promotes soil carbon and nitrogen stocks in grasslands without legumes,
606 *Journal of Ecology* **102:** 1163-1170.

Costanzo, A, Barberi, P. 2014. Functional agrobiodiversity and agroecosystem services in sustainable wheat production. A review. *Agronomy for Sustainable Development* **34:** 327-348.

De Barros I, Gaiser T, Lange FM, Romheld V 2007. Mineral nutrition and water use patterns of a maize/cowpea intercrop on a highly acidic soil of the tropic semiarid. *Field Crops Research* **101:** 26-36.

De Deyn GB, Cornelissen JH, Bardgett RD 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters* **11:** 516-531.

De Deyn GB, Shiel RS, Ostle NJ, McNamara NP, Oakley S, Young I, Freeman C, Fenner N, Quirk H, Bardgett RD 2011. Additional carbon sequestration benefits of grassland diversity restoration. *Journal of Applied Ecology* **48:** 600-608.

Duivenbooden N Van, Pala N, Studer C, Bielders CL, Beukes DJ. 2000. Cropping systems and crop complementarity in dryland agriculture to increase soil water use efficiency: a review. *NJAS - Wageningen Journal of Life Sciences* **48:** 213–236.

Dupraz C, Liagre F. 2011. *Agroforesterie – des arbres et des cultures*, *2^{e} édition*. Paris, France : Groupe France Agricole.

Eichhorn MP, Paris P, Herzog F, Incoll LD, Liagre F, Mantzanas K, Mayus M, Moreno G, Papanastasis VP, Pilbeam DJ *et al.* 2006. Silvoarable systems in europe - past, present and future prospects. *Agroforestry Systems* **67:** 29-50.

Ehrmann, J. Ritz, K. 2014. Plant: soil interactions in temperate multi-cropping production systems. *Plant and Soil* **376:** 1-29.

Feike T, Doluschitz R, Chen Q, Graeff-Hönninger S, Claupein W. 2012. How to overcome the slow death of intercropping in the North China Plain. *Sustainability* **4:** 2550-2565.

Fernandes MF, Barreto AC, Mendes IC, Dick RP. 2011. Short-term response of physical and chemical aspects of soil quality of a kaolinitic Kandiudalfs to agricultural practices and its association with microbiological variables. *Agriculture, Ecosystems and Environment* **142:** 419-427.

Finch S, Collier RH. 2012. The influence of host and non-host companion plants on the behaviour of pest insects in field crops. *Entomologia Experimentalis et Applicata* **142:** 87–96.

Francis CA. 1986. Introduction: distribution and importance of multiple cropping. In: Francis CA, ed. *Multiple Cropping Systems.* New York, USA: MacMillan Publishing Company, 1-19.

Frimpong EA, Gemmill-Herren B, Gordon I, Kwapong PKI. 2011. Dynamics of insect pollinators as influenced by cocoa production systems in Ghana. *Journal of Insect Pollination* **5:** 74-80.

Garcia-Pausas J, Paterson E 2011. Microbial community abundance and structure are determinants of soil organic matter mineralisation in the presence of labile carbon. *Soil Biology and Biochemistry* **43:** 1705-1713.

George TS, Hawes C, Newton AC, McKenzie BM, Hallett PD, Valentine TA. 2014. Field phenotyping and long-term platforms to characterise how crop genotypes interact with soil processes and the environment. *Agronomy* **4:** 242-278.

Goulson D, Lye, GC, Darvill B. 2008. Decline and conservation of bumble bees. *Annual Review of Entomology* **53:** 191-208.

Grace JB. 2006. *Structural Equation Modelling and Natural Systems*. Cambridge, UK: Cambridge University Press.

Gregory AS, Watts CW, Griffiths BS, Hallett PD, Kuan HL, Whitmore AP 2009. The effect of long-term soil management on the physical and biological resilience of a range of arable and grassland soils in England. *Geoderma* **153:** 172-185.

Hallett PD, Bengough AG. 2013. Managing the soil physical environment for plants. In: Gregory PJ, Nortcliff S. eds. *Soil Conditions and Plant Growth*. Chichester, UK: Wiley-Blackwell, 238-268.

Handa IT, Aerts R, Berendse F, Berg MP, Bruder A, Butenschoen O, Chauvet E, Gessner MO, Jabiol J, Makkonen M *et al.* 2014. Consequences of biodiversity loss for litter decomposition across biomes. *Nature* **509**: 218-221.

Harris D, Fry GJ, Miller ST. 1994. Microtopography and agriculture in semi-arid Botswana. 2. Moisture availability, fertility and crop performance. *Agricultural Water Management* **26:** 133-148.

Hauggaard-Nielsen H, Ambus P, Jensen ES. 2001. Temporal and spatial distribution of roots and competition for nitrogen in pea-barley intercrops – a field study employing ^{32}P technique. *Plant and Soil* **236:** 63-74.

Hauggaard-Nielsen H, & Jensen ES. 2005. Facilitative root interactions in intercrops. *Plant and Soil* **274:** 237–250.

Hauggaard-Nielsen H, Gooding M, Ambus P, Corre-Hellou G, Crozat Y, Dahlmann C, Dibet A, von Fragstein P, Pristeri A, Monti M *et al.* 2009. Pea-barley intercropping for efficient symbiotic N_2 fixation, soil N acquisition and use of other nutrients in European organic cropping systems. *Field Crops Research* **113:** 64-71.

He JB, Bögemann GM, van de Steeg HM, Rijnders JGHM, Voesenek LACJ, Blom CWPM. 1999. Survival tactics of *Ranunculus* species in river floodplains. *Oecologia* **118:** 1-8.

He Q, Bertness MD, Altieri AH. 2013. Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters* **16:** 695-706.

Henriksen CB, Mølgaard, JP, Rasmussen, J. 2007. The effect of autumn ridging and inter-row subsoiling on potato tuber yield and quality on a sandy soil in Denmark. *Soil and Tillage Research* **93:** 309-315.

Hill, J. 1996. Breeding components for mixture performance. *Euphytica* **92:** 135-138.

Hortal S, Bastida F, Lozano MY, Armas, C, Moreno JL, Pugnaire FI. 2013. Soil microbial community under a nurse-plant species changes in composition, biomass and activity as the nurse grows. *Soil Biology & Biochemistry* **64:** 139-146.

Huston, MA. 1997. Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia* **110:** 449-460.

Iannetta PPM, Begg G, James EK, Smith B, Davies C, Karley A, Lopez Del Egido L, Hawes C, Young M, Ramsay G *et al.* 2013. Sustainable intensification: a pivotal role for legume supported crop systems. *Aspects of Applied Biology* 121: 73-82.

Inal A, Gunes A. 2008. Interspecific root interactions and rhizosphere effects on salt ions and nutrient uptake between mixed grown peanut/maize and peanut/barley in original saline-sodic-boron toxic soil. *Journal of Plant Physiology* **165**: 490-503.

Kanton RAL, Dennett MD. 2008. Radiation capture and use as affected by morphologically contrasting Maize/Pea in sole and intercropping. *West African Journal of Applied Ecology* **13: 55-66**.

Johnson WG, Davis VM, Kruger GR, Weller SC. 2009. Influence of glyphosate-resistant cropping systems on weed species shifts and glyphosate-resistant weed populations. *European Journal of Agronomy* **31:** 162-172.

Kremen C, Williams NM, Thorp RW. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Science of the USA* **99:** 16812-16816.

Lawrence D, Fiegna F, Behrends V, Bundy JG, Phillimore AB, Bell T, Barraclough TG. 2012. Species interactions alter evolutionary responses to a novel environment. *PLoS Biology* **10:** e1001330.

Letourneau D, Armbrecht I, Salguero Rivera B, Lerma JM, Jimenez Carmona E, Constanza Daza M, Escobar S, Galindo V, Gutierrez C, Duque Lopez S *et al.* 2011. Does plant diversity benefit agroecosystems? A synthetic review. *Ecological Applications***21:** 9-21.

Li L, Li SM, Sun JH, Zhou LL, Bao XG, Zhang HG, Zhang FS. 2007. Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. *Proceedings of the National Academy of Sciences of the USA* **104:** 11192-11196.

Li L, Zhang L-Z, Zhang F-Z. 2013. Crop mixtures and the mechanisms of overyielding. In: Levin SA, ed. *Encyclopedia of Biodiversity, Second edition, Volume 2*. Waltham, MA, USA: Academic Press, 382-395.

Li L, Tilman D, Lambers H, Zhang F-S. 2014. Biodiversity and overyielding: Insights from below-ground facilitation of intercropping in agriculture. *New Phytologist* **203**: 63-69.

Li YF, Ran W, Zhang RP, Sun SB, Xu GH. 2009. Facilitated legume nodulation, phosphate uptake and nitrogen transfer by arbuscular inoculation in an upland rice and mung bean intercropping system. *Plant and Soil* **315:** 285-296.

Lithourgidis, AS, Dordas, CA, Damalas, CA, Vlachostergios, DN. 2011. Annual intercrops: an alternative pathway for sustainable agriculture. *Australian Journal of Crop Science* **5:** 396-410.

Loomis, RS, Connor, DJ. 1992. *Crop Ecology: Productivity and Management in Agricultural Systems.* Cambridge, UK: Cambridge University Press.

Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412:** 72–76.

724 **Mace GM, Norris K, Fitter AH. 2012.** Biodiversity and ecosystem services: a multilayered
725 relationship. *Trends in Ecology & Evolution* **27:** 24-31.
726 **Mao LL, Zhang LZ, Li WQ, van der Werf W, Sun JH, Spiertz H, Li L. 2012.** Yield advantage and
727 water saving in maize/pea intercrop. *Field Crops Research* **138:** 11-20.
728 **Marschner P. 2012. (Ed.)** *Mineral Nutrition of Higher Plants*, *3rd edn.* Waltham, MA, USA:
729 Academic Press.
730 **Morris RA, Garrity DP. 1993.** Resource capture and utilization in intercropping-Water. *Field*
731 *Crops Research* **34:** 303-317.
732 **Naeem S, Li S. 1997.** Biodiversity enhances ecosystem reliability. *Nature* **390:** 507-509.
733 **Ngwira AR, Aune JB, Mkwinda S. 2012.** On-farm evaluation of yield and economic benefit of
734 short term maize legume intercropping systems under conservation agriculture in Malawi.
735 *Field Crops Research* **132,** 149-157.
736 **Obalum SE, Obi ME. 2010.** Physical properties of a sandy loam Ultisol as affected by tillage-
737 mulch management practices and cropping systems. *Soil and Tillage Research* **108**: 30-36.
738 **Odum EP. 1968.** *Fundamentals of Ecology, 2nd edn.* London, UK: Saunders.
739 **Oerke E.-C. 2006.** Crop losses to pests. *Journal of Agricultural Science* **144:** 31-43.
740 **Orrell P, Bennett AE. 2013.** How can we exploit above-belowground interactions to assist in
741 addressing the challenges of food security? *Frontiers in Plant Science* **4:** 432
742 (doi:10.3389/fpls.2013.00432)
743 **Pappa VA, Rees RM, Walker RL, Baddeley JA, Watson CA. 2011.** Nitrous oxide emissions
744 and nitrate leaching in an arable rotation resulting from the presence of an intercrop.
745 *Agriculture, Ecosystems and Environment* **141:** 153-161.

Pappa, VA, Rees, RM, Walker, RL, Baddeley, JA, Watson, CA. 2012. Legumes intercropped with spring barley contribute to increased biomass production and carry-over effects. *Journal of Agricultural Science* **150:** 584-594.

Pérès G, Cluzeau D, Menasseri S, Soussana JF, Bessler H, Engels C, Habekost M, Gleixner G, Weigelt A, Weisser WW *et al*. 2013. Mechanisms linking plant community properties to soil aggregate stability in an experimental grassland diversity gradient. *Plant and Soil* **373:** 285-299.

Postma J, Lynch JP. 2012. Complementarity in root architecture for nutrient uptake in ancient maize/bean and maize/bean/squash polycultures. *Annals of Botany* **110:** 521-534.

Potts SG, Vulliamy B, Dafni A, Ne'eman G, Willmer PG. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology* **84:** 2628–2642.

Powlson DS, Gregory PJ, Whalley WR, Quinton JN, Hopkins DW, Whitmore AP, Hirsch PR, Goulding KWT. 2011. Soil management in relation to sustainable agriculture and ecosystem services. *Food Policy*, **36**: S72-S87.

Prieto I, Armas C, Pugnaire FI. 2012. Water release through plant roots: new insights into its consequences at the plant and ecosystem level. *New Phytologist* **193:** 830-841.

Rao R, Li Y. 2003. Management of flooding effects on growth of vegetable and selected field crops. *HortTechnology* **13**: 610-616.

Reich PB, Tilman D, Isbell F, Mueller K, Hobbie SE, Flynn DFB, Eisenhauer N. 2012. Impacts of biodiversity loss escalate through time as redundancy fades. *Science* **336:** 589–592.

Rusinamhodzi L, Corbeels M, Nyamangara J, Giller KE. 2012. Maize–grain legume intercropping is an attractive option for ecological intensification that reduces climatic risk for smallholder farmers in central Mozambique. *Field Crops Research* **136:** 12-22.

Ryan PR, Tyerman SD, Sasaki T, Furuichi T, Yamamoto Y, Zhang WH, Delhaize E. 2011. The identification of aluminium-resistance genes provides opportunities for enhancing crop production on acid soils. *Journal of Experimental Botany* **62:** 9-20.

Schmidt W. 2013. Experiences from organic maize breeding and prospects of coevolutionary breeding. In: *Abstracts of the EUCARPIA Meeting "Breeding for Nutrient Efficiency"*, Göttingen, Germany, 24 – 26 September 2013. (http://www.uni-goettingen.de/de/415791.html)

Schöb C, Callaway RM, Anthelme F, Brooker RW, Cavieres LA, Kikvidze Z, Lortie CJ, Michalet R, Pugnaire FI, Xiao S *et al*. 2014. The context dependence of beneficiary feedback effects on benefactors in plant facilitation. *New Phytologist* **204:** 386-396.

Schuh WM, Meyer RF, Sweeney, MD, Gardner J. 1993. Spatial variation of root-zone and shallow vadose-zone drainage on a loamy glacial till in a sub-humid climate. *Journal of Hydrology* **148:** 1–26.

Seran TH, Brintha I. 2010. Review on maize based intercropping. *Journal of Agronomy* **9:** 135-145.

Shackel KA, Hall AE. 1984. Effect of intercropping on the water relations of sorghum and cowpea. *Field Crops Research* **8:** 381-387.

Shen JB, Yuan LX, Zhang JL, Li HG, Bai ZH, Chen XP, Zhang WF, Zhang FS. 2011. Phosphorus dynamics: from soil to plant. *Plant Physiology* **156:** 997-1005

Shen JB, Li CJ, Mi GH, Li L, Yuan LX, Jiang RF, Zhang FS. 2013. Maximizing root/rhizosphere efficiency to improve crop productivity and nutrient use efficiency in intensive agriculture of China. *Journal of Experimental Botany* **64:** 1181-1192.

Simões CC, Melo JO, Magalhaes JV, Guimarães CT. 2012. Genetic and molecular mechanisms of aluminum tolerance in plants. *Genetics and Molecular Research* **11:** 1949-57.

Smith J, Pearce BD, Wolfe M, Martin S. 2013. Reconciling productivity with protection of the environment: Is temperate agroforestry the answer? *Renewable Agriculture and Food Systems* **28:** 80-92.

Smith SE, Read DJ. 2008. *Mycorrhizal Symbiosis*. New York, USA: Academic Press.

Swinton SM, Lupi F, Robertson GP, Hamilton SK. 2007. Ecosystem services and agriculture: Cultivating agricultural ecosystems for diverse benefits. *Ecological Economics* **64**: 245–252.

Tisdall JM, Adem HH. 1990. Mechanised relay-cropping in an irrigated red-brown earth in south-eastern Australia. *Soil Use and Management* **6:** 21-28.

Tong PY. 1994 Achievements and perspectives of tillage and cropping systems in China (in Chinese). *Cropping System and Cultivation Technology (Genzuo Yu Zaipei)* **77:** 1-5.

Trenbath BR. 1974. Biomass productivity of mixtures. *Advances in Agronomy* **26:** 177-210.

Trinder C, Brooker R, Davidson H, Robinson D. 2012. Dynamic trajectories of growth and nitrogen capture by competing plants. *New Phytologist* **193:** 948-958.

Van der Heijden MGA, Horton TR. 2009. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *Journal of Ecology* **97:** 1139-1150.

Van der Heijden MGA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396:** 69-72.

Van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA *et al*. 2013. Plant-soil feedbacks: the past, the present and future challenges. *Journal of Ecology* **101:** 265-276.

Vandermeer JH. 1989. *The Ecology of Intercropping*. Cambridge, UK: Cambridge University Press.

Vandermeer J. 2010. *The Ecology of Agroecosystems*. Sudbury, MA, USA: Bartlett and Jones.

817 **Wäckers FL. 2004.** Assessing the suitability of flowering herbs as parasitoid food sources:
818 flower attractiveness and nectar accessibility. *Biological Control* **29:** 307-314.
819 **Walder F, Niemann H, Natarajan M, Lehmann MF, Boller T, Wiemken A. 2012.** Mycorrhizal
820 networks: Common goods of plants shared under unequal terms of trade. *Plant Physiology*
821 **159:** 789-97.
822 **White PJ, George TS, Dupuy LX, Karley AJ, Valentine TA, Wiesel L, Wishart J. 2013a.** Root
823 traits for infertile soils. *Frontiers in Plant Science* **4:** 193 (doi: 10.3389/fpls.2013.00193).
824 **White PJ, George TS, Gregory PJ, Bengough AG, Hallett PD, McKenzie BM. 2013b.** Matching
825 roots to their environment. *Annals of Botany* **112:** 207-222.
826 **White PJ, Greenwood DJ. 2013.** Properties and management of cationic elements for crop
827 growth. In: Gregory PJ, Nortcliff S. eds. *Soil Conditions and Plant Growth*. Oxford, UK:
828 Blackwell Publishing, 160-194.
829 **Wojtkowski PA. 2006.** *Introduction to Agroecology: Principles and Practices*. Binghampton,
830 NY, USA: Food Products Press.
831 **Xiao YB, Li L, Zhang FS. 2004.** Effect of root contact on interspecific competition and N
832 transfer between wheat and faba bean using direct and indirect ^{15}N techniques. *Plant and*
833 *Soil* **262:** 45-54.
834 **Xu BC, Li FM, Sham L. 2008.** Switchgrass and milkvetch intercropping under 2:1 row-
835 replacement in semiarid region, northwest China: aboveground biomass and water use
836 efficiency. *European Journal of Agronomy* **28:** 485–492.
837 **Zegada-Lizarazu W, Izumi Y, Iijima M. 2006.** Water competition of intercropped pearl millet
838 with cowpea under drought and soil compaction stresses. *Plant Production Science* **9:** 123-
839 132.

Zhang F, Shen J, Zhang J, Zuo Y, Li L, Chen X. 2010. Rhizosphere processes and management for improving nutrient use efficiency and crop productivity: Implications for China. *Advances in Agronomy* **107:** 1-32.

Zhang K, Greenwood DJ, White PJ, Burns IG. 2007. A dynamic model for the combined effects of N, P and K fertilizers on yield and mineral composition; description and experimental test. *Plant and Soil* **298:** 81-98.

Zhu YY, Chen HR, Fan JH, Wang YY, Li Y, Chen JB, Fan JX, Yang SS, Hu LP, Leung H *et al.* 2000. Genetics diversity and disease control in rice. *Nature* **406:** 718-722.

Zomer RJ, Trabucco A, Coe R, Place F. 2009. Trees on Farm: Analysis of Global Extent and Geographical Patterns of Agroforestry. *ICRAF Working Paper no. 89.* Nairobi, Kenya: World Agroforestry Centre.

Zuo Y, Zhang F. 2011. Soil and crop management strategies to prevent iron deficiency in crops. *Plant and Soil* **339:** 83-95.

Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Examples of the types and scales of benefits and dis-benefits found in intercropping experiments and trials.

859 **Figure Legends**

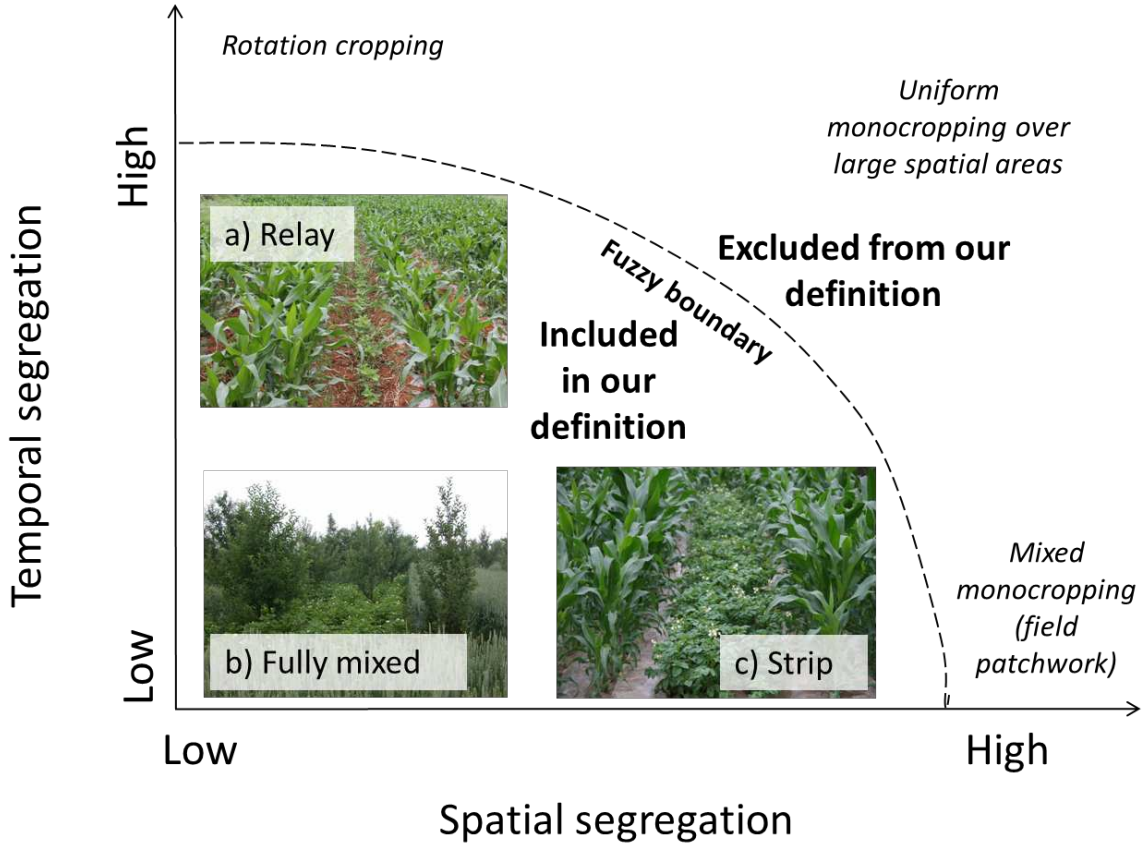
860 **Figure 1.** Representation of the distinction - depending on the degree of both the spatial (x-
861 axis) and temporal (y-axis) segregation of two (or more) crop species - between
862 intercropping and other cropping systems. The figure also shows those crop types that are
863 explicitly excluded from our definition of an intercropping system, but also that there is a
864 "fuzzy boundary" between what might and might not be considered an intercropping
865 system. Images illustrate three broad types of intercrop: a - relay intercropping (maize and
866 soy bean, with Soy bean planted later, Yunnan Province, Southwest China; photo Wen-Feng
867 Cong), b - fully mixed (e.g. homegarden) intercropping (Gansu, China; photo Long Li), c –
868 strip intercropping (maize and potato, Gansu, China; photo Jianbo Shen).

869

870 **Figure 2.** Facilitation, resource sharing, and niche complementarity enable polyculture
871 systems to yield more than their corresponding monocultures. Certain facilitative
872 interactions can be associated with particular soil types (either acid soils, or alkaline and
873 calcareous soils), and when present can be either strong (soil lines) or weak (dashed lines).
874 Facilitation is achieved by combining plants that increase the phytoavailability of water,
875 phosphorus (P) or micronutrients (Fe, Zn, Cu) or the nitrogen (N) available to the system
876 through N_2 fixation either directly or indirectly (Zhang *et al.,* 2010; Shen *et al.,* 2013; White
877 *et al.,* 2013a, b; Li *et al.*, 2014), through the attraction of beneficial organisms, such as
878 natural enemies and pollinators, the deterrence of pests and pathogens and the suppression
879 of weeds. Facilitative interactions between plant roots can also afford protection against
880 mineral toxicities in saline, sodic or metalliferous soils (Inal & Gunes, 2008; White &
881 Greenwood, 2013). Resource sharing can be affected through common mycorrhizal fungal
882 networks (van der Heijden & Horton, 2009; Walder *et al.*, 2012; Babikova *et al.*, 2013) or

883 recycling of nutrients through leaf senescence and root turnover (Zhang *et al.,* 2010; Li *et*
884 *al.*, 2014). Niche complementarity, which allows maximal exploitation of light and soil
885 resources, is observed between species with contrasting short and tall shoot architectures,
886 or shallow and deep root architectures (Hauggaard-Nielsen *et al.*, 2001; Zhang *et al.,* 2010;
887 Postma & Lynch, 2012). It is also apparent when plants acquire mineral elements in different
888 chemical forms. The net benefits are crop protection, pollination, greater photosynthetic
889 carbon assimilation, greater acquisition of N, P, micronutrient and water, and sharing of
890 these resources temporally to increase yield. These benefits lead to enhanced resource use
891 efficiencies for P (PUE), N (NUE), other mineral nutrients (MUE), water (WUE), light (LUE)
892 and assimilates (RUE).
893
894 **Figure 3.** Examples of recent developments in ecological research (top row) and their
895 relevance to important goals for the improvement of intercropping systems (middle row),
896 leading to the final aim of improved intercropping systems as measured through a number
897 of performance metrics (bottom row). In addition, on-going ecological research has
898 considerable potential to discover novel interaction processes, which could improve our
899 understanding of trait complementarity or interaction context-dependency, or could help us
900 improve intercropping systems in as yet unknown ways as indicated by the dashed lines and
901 arrows.
902

903 **Brooker et al., Figure 1**



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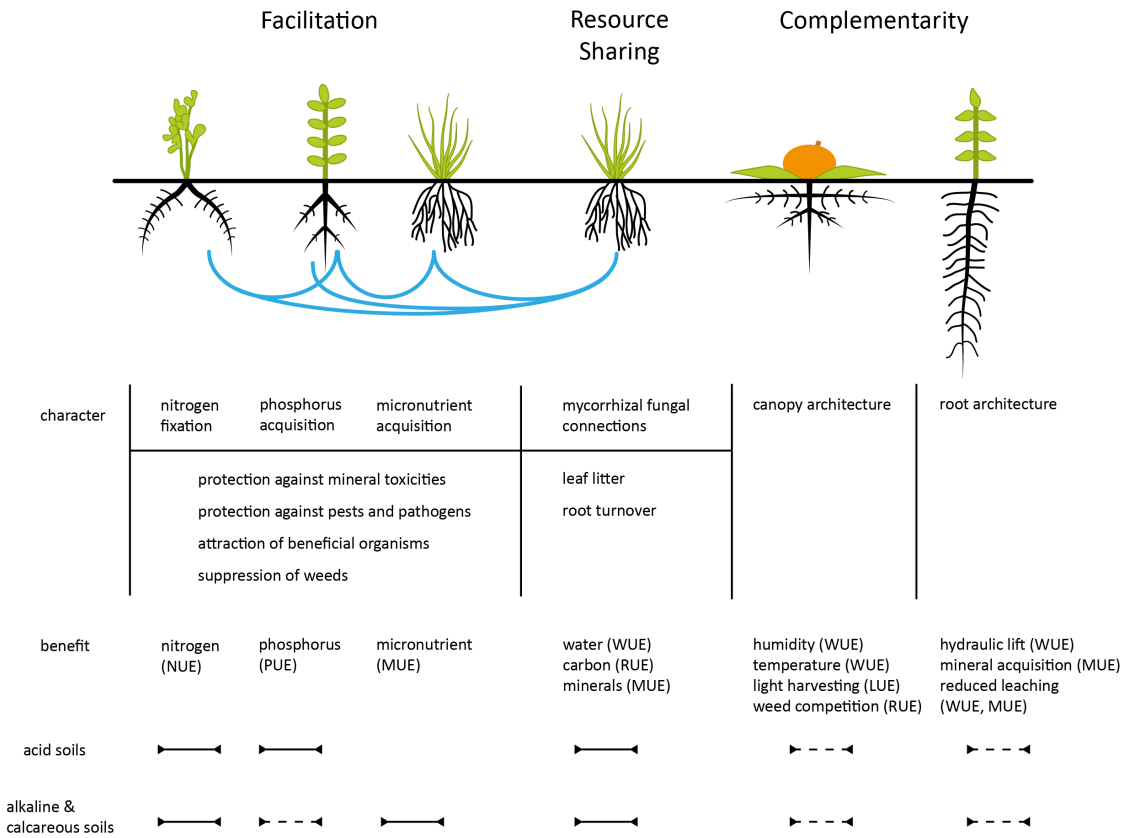
905

906 **Brooker et al. Figure 2**



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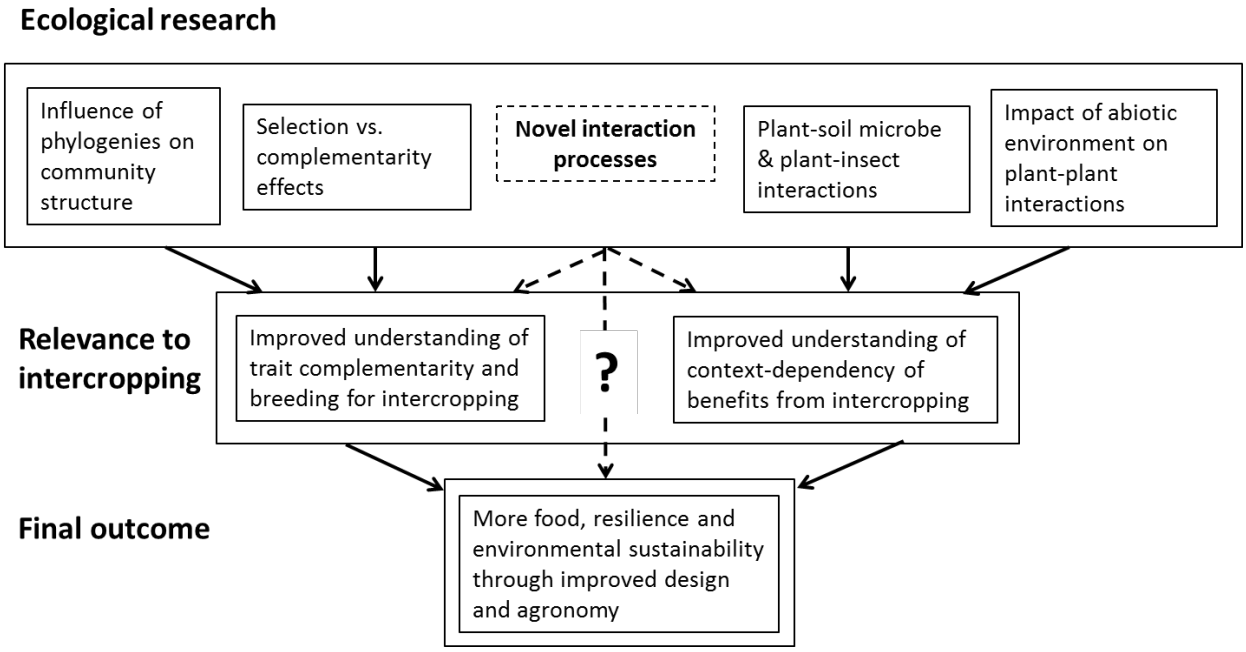
908

Brooker et al. Figure 3



Brooker et al. Supporting Information Table S1

Examples of the types and scales of benefits and dis-benefits found in intercropping experiments and trials, along with information on their underlying mechanisms. The Table shows the effect type (in bold; for example the impacts on light capture or nutrient use efficiency and availability) and the original source of the information, the source of the information provided here (for example, if the presented data have been taken from a review paper rather than the original study), the type of crop system studied, the region and/or country in which the study was undertaken, details of the benefit or dis-benefit found by the study (including impacts on LER – Land Equivalent Ratio - when not in the *Yield volume and quality* category) and more detail on the underlying mechanism (plus any relevant notes to aid interpretation).

Benefit type and original paper	Source of information provided here	Crop system studied	Region and/or Country	Benefit or dis-benefit & mechanisms
Light capture				
Bedoussac & Justes (2010)		Durum wheat-winter pea	Auzeville, France	Intercropping system had up to 10% greater light capture.
Ghanbari *et al.* (2010)		Maize-cowpea	Zabol, Iran	Additive design intercropping increased the absorption of photosynthetically active radiation (PAR) by 11.1% as compared with sole maize, but reduced it by 14.8% as compared with sole cowpea.
Szumigalski & van Acker (2008)		Wheat-canola-field pea,canola-field pea	Manitoba, Canada	Intercropping increased radiation use efficiency: light interception was increased by 24% (wheat-pea intercropping), by 49% (canola-pea), and by 55% (wheat-canola-pea) compared with sole wheat.
Nutrient use efficiency and availability				
Garrity *et al.* (2010)	Li *et al.* (2013)	Various	Various	Soil nitrogen content increases in intercrops ranged from 15% to 156%; significant increases were also found in C, P exchangeable K, Ca, and Mg. Data from a review of the impact on associated crops of intercropping with the leguminous tree *Faidherbia albida*
Gunes *et al.* (2007)		Chickpea-barley	Glasshouse trial	When intercropped, biomass yield of barley increased whilst that of chickpea decreased. Rhizosphere acidification by chickpea increased available P and Fe concentrations, and physiological responses (e.g. an increase in P concentration of intercropped barley plants from 1.48 to 1,.53 g kg^{-1}) indicate that mixed cropping with chickpea may improve P nutrition of barley.
Hauggaard-Nielsen *et al.* (2001)	Ehrmann & Ritz (2014)	Pea-barley intercrop	Roskilde, Denmark	Compared to pea sole crop, there were 40-80% increases in N_2 fixation in the intercrop, with up to 95% of the total pea N in the intercrop being derived from the atmosphere.
Inal & Gunes (2008)		Peanut-maize and peanut-barley	Glasshouse trial	When grown in intercrops in saline-sodic soils (which contain an excess of Na) and B toxic soils, peanut facilitated P nutrition of maize and barley, while maize and barley improved K, Fe, Zn and Mn nutrition of peanut.

Li *et al.* (2001)	Zhang & Li (2003)	Wheat-maize	Wuwei, Gansu, in Hexi corridor, northwest China	Intercrops showed less nitrate accumulation in the soil profile: levels under the intercrop compared to sole wheat were 0-41% lower.
Li *et al.* (2001)	Zhang & Li (2003)	Faba bean-maize	Wuwei, in Hexi corridor, northwest China	Intercrops showed less nitrate accumulation in the soil profile: levels under the intercrop compared to sole fava bean were 0-31% lower.
Li *et al.* (2002)	Zhang & Li (2003)	Maize-faba bean	Jinyuan, Gansu, China	Changes in nutrient uptake depending on root mixing. When roots intermingled N uptake was 38.4 g N m^{-2} and P uptake was 4.2 g P m^{-2} (with an LER of 1.21); when roots were artificially separated N uptake was 31.8 g N m^{-2}, P uptake was 3.3 g P m^{-2} (with an LER of 1.06).
Pappa *et al.* (2011)		Barley -pea	Eastern Scotland	N loss was reduced under the intercrop when compared with the barley monocrop: cumulative values for nitrate leaching for intercrop and monocrop were 0.67 and 3.80 kg NO_3−N ha^{-1}, respectively; cumulative N_2O emissions were 1.3 kg N ha^{-1} from the barley monocrop and 1.0 kg N ha^{-1} from the barley-pea intercrop.
Xia *et al.* (2013)		Canola-maize; Chickpea-maize; faba bean-maize; soybean-maize intercropping	Gansu, China	Intercropping enhanced recovery of P fertilizers. Average enhancement (over three years) of P recovery in intercropping compared to monocropping systems was between 6.1% to 30.6% at 40 kg P ha^{-1} and between 4.8% to 14.5% at 80 kg P ha^{-1}.
Xiong *et al.* (2013)		Peanut-maize	Glasshouse trial	Peanut and maize were intercropped in calcareous soils; intercropping enhanced maize phytosiderophore release rate approximately three-fold, which is likely to benefit peanut Fe acquisition. Peanut intercropped with phytosiderophores-releasing mutant maize ys3 (i.e. a mutant unable to release phytosiderophores) exhibited Fe deficient chlorosis.

Pest, disease and weed control

Andow 1991	Lithourgidis *et al.* (2011)	Various	Various	Out of 287 pest species examined, the population of pest species was lower in the intercrop compared to the relevant monocrops in 52% of studies (149 spp. - 60% monophagous and 28% polyphagous) and higher in 15% of the studies (44 spp.). Data from a review of 209 studies.
Andow 1991	Lithourgidis *et al.* (2011)	Various	Various	Populations of natural enemies of pests were higher in the intercrop compared the relevant monocrops in 53% of studies, and lower in 9%. Data from a review of 209 studies.
Baumann *et al.* (2000)	Lithourgidis *et al.* (2011)	Leek-celery	Wädenswil, Switzerland	Relative soil cover of weeds that emerged at the end of the critical period for weed control was reduced by 41% in the intercrop.
Chen *et al.* (2007)		Wheat-faba bean	Yunnan Province, China	Wheat powdery mildew incidence was not significantly different between monoculture and intercropping plots. But disease incidence increased as nitrogen application increased. With nitrogen increasing from 0 to 150 and 300 kg N ha^{-1}, the wheat powdery milder incidence increased from 48.3% to 93.3% and 95.0%, respectively, with the disease severity index ranging from 6.7% to 26.7% to 30.7%, respectively.

Corre-Hellou *et al.* (2011)		Pea-barley	Organic field experiments across western Europe (Denmark, UK, France, Germany and Italy)	Weed biomass was 3 times higher under the pea sole crops than under both the intercrops and barley sole crops at maturity.
Finckh *et al.* (2000)		Cereal variety and species mixtures	Various	The most important mechanisms reducing disease in variety and species mixtures are barrier and frequency effects, and induced resistance. Differential adaptation, i.e. adaptation within races to specific host genotypic backgrounds, may prevent the rapid evolution of complex pathotypes in mixtures. Data from a review of 68 studies.
Fininsa (1996)	Lithourgidis *et al.* (2011)	Bean-maize	Alemaya, Ethiopia	Common bacterial blight incidence levels were reduced in mixed cropping by an average of 23% (compare to monocropping) and 5% (compared to row intercropping); Mixed intercropping reduced rust incidence by 51% (compared to sole cropping) and 25% (compared to row intercropping)
Gliessman, 1983		Maize-bean-squash	California, USA	The intercrop reduced the total dry mass of four common weed species (*Plantago lanceolata*, *Chenopodium album*, *Spergula arvensis*, and *Rhaphanus sativa*) by 62.5% compared to weed biomass in maize monoculture.
Hummel *et al.* (2009)		Canola-wheat	Alberta, Canada	Even though the proportions of pathogen-infected wheat leaf tissue were up to 2.5 times greater in intercrops than in wheat monocultures, the LER was close to one, indicating the disease occurrence did not affect intercropping yield.
Li *et al.* (2009)	Li *et al.* (2013)	Tobacco-maize, sugarcane-maize, potato-maize and wheat-faba bean	Yunnan Province, China	Intercropped plots showed reductions in the severity of a range of diseases in 2006 and 2007 compared to sole crop plots: northern maize leaf blight - 17.0% and 19.7%; tobacco brown leaf spot - no difference; potato late blight - 32.9% and 39.4%; broad (i.e. fava) bean chocolate spot disease - 33.8% and 31.7%
Poggio (2005)		Field pea-barley	Aries and Rojas, Argentina	Weed species richness in polyculture, barley or pea plots was depressed by 32.8%, 43.5% or 48.9%, respectively, and weed community (Shannon) evenness was reduced by 67.9%, 96.4% and 96.4%, respectively, compared to values for uncropped plots.
Risch (1983)	Lithourgidis *et al.* (2011)	Various	Various	Out of 198 herbivore species included in the review 53% of the pest species were less abundant in the intercrop, 18% were more abundant, 9% showed no significant difference, and 20% showed a variable response. Data from a review of 150 studies.
Saucke & Ackermann (2006)	Lithourgidis *et al.* (2011)	Pea-false flax	Hebenshausen, Germany	Intercrops had a greater suppressive effect on weed cover compared to monocrops of 63% and 52% in 2003 and 2004, respectively.
Zeller *et al.* (2012)		Genetically modified wheat line mixture	Zurich-Reckenholz, Switzerland,	Resistance to mildew increased with GM richness. Plots with two transgenes had 34.6% less mildew and 7.3% higher seed yield than plots with one transgene. GM richness indicates the number of *Pm3* transgenes with different mildew specifities per plot.
Zhu *et al.* (2000)		Rice-rice	Yunnan Province, China	Blast severity of rice grown in mixture was reduced by 94% compared to rice in monoculture

Water use efficiency, and runoff quality and volume

Caviglia *et al.* (2004)	Li *et al.* (2013)	Wheat-soybean	South-eastern Pampas	Water capture in intercrop was 604-609 mm compared to 313-334 mm for sole wheat and 359-434 mm for sole soybean.
Gao *et al.* (2009)	Li *et al.* (2013)	Winter wheat-spring maize	Huang-Huai-Hai Plain, China	Water use efficiency was 21.72 kg ha^{-1} mm^{-1} - this is 23% less than that of sole maize, but 4% greater than that of sole wheat. Note that this is a potentially negative effect. However, the conclusion as summarised by Li et al. is that although the intercropping system does not improve WUE, it may significantly raise yield.
Kanwar *et al.* (2005)	Li *et al.* (2013)	Maize-soybean	Iowa, USA	Nitrate N leaching losses were reduced by 6% (and maize grain yields increased by 5%) in the intercrop compared to the monocrops.
Mao *et al.* (2012)		Maize-pea	Gansu, China	Intercropping of maize and pea altered the Water Efficiency Ratio - characterizing the water use efficiency of intercropping in a manner analogous to LER – which ranged from 0.87 to 1.16 (LER ranged from 1.18 to 1.47).
Yang *et al.* (2011)		Wheat-maize	Gansu, China	In a three year field study wheat-maize intercropping treatments increased total water use by 1.8-16.4% compared to sole-cropping wheat and maize. However, water use efficiency (WUE) of intercropping was increased significantly in all three years compared to sole cropped wheat (average increase of 29.1%), and compared to sole maize it was increased significantly in one of the study years (by 35.0%).
Zougmore *et al.* (2000)	Lithourgidis *et al.* (2011)	Sorghum-cowpea	Central Plateau, Burkina Faso	The intercrop reduced run-off by 20-30% and 45-55% compared with sorghum and cowpea monocrops, respectively; soil loss was reduced with intercropping by more than 50%.

Yield volume and quality

Chen *et al.* (2004)	Lithourgidis *et al.* (2011)	Barley-Austrian winter pea	Montana, USA	The intercrop had a LER of 1.05-1.24 on a biomass basis and 1.05-1.26 on a protein basis.
Dhima *et al.* (2013)		Oat-faba bean	Northern Greece	Intercrops provided higher total dry matter and protein yields than those of faba bean sole crops (for example at a 50:50 sowing ratio, between 12 and 58% higher dry matter and 11-39% higher protein), but lower or similar yields to those of oat sole crops (between 51% less and 2.73% more dry matter, and 47% less and 7% more protein).
Dordas & Lithourgidis (2011)		Faba bean-triticale	Northern Greece	Forage dry matter was increased by 37% in the intercrop, with a 12% increase in crude protein yield per hectare compared to the faba bean monocrop.
Gaffarzadeh *et al.* (1994)	Zhang & Li (2003)	Maize-soybean strip intercropping	Iowa, USA	In the intercrop there was 20-24% greater maize production and 10-15% lower soybean production in adjacent border rows.
Garrity *et al.* (2010)	Li *et al.* (2013)	Various	Various	In the intercrop millet yields increased by 49% to 153%, and sorghum from 36% to 169% (in asbolute terms an additional cereal yield of 400-500 kg/ha or more). Data from a review of the impact on associated crops of intercropping with the leguminous tree *Faidherbia albida*.
Li *et al.* (2001)	Zhang & Li (2003)	Wheat-maize	Wuwei, Gansu, in Hexi corridor, northwest China	In the intercrop there was a 74% increase in grain yield of wheat; maize response is not specified.

Li *et al.* (2001)	Zhang & Li (2003)	Wheat-soybean	Jinyuan, Gansu, China	In the intercrop there was a 53% increase in grain yield of wheat; the soybean response is not specified.
Li *et al.* (2007)		Fababean- maize	Baiyun Experimental Site, Western Gansu Province, China	In the intercrop maize over-yielded by 43% (17-74%) and faba bean by 26% (3-33%); over-yielding was more consistent in maize.
Li *et al.* (2007)		Faba bean- maize cf maize-wheat	Baiyun Experimental Site, Western Gansu Province, China	Under low P_2O_5 applications of 0, 37.5, and 75 kg/ha, maize grain yield in the fababean-maize compared to the wheat-maize intercrop was increased by 35% (P<.10), 40% (P<0.10) and 25% (P<0.05), respectively. Under high P_2O_5 applications (112.5 and 150 kg/ha) maize grain yield did not differ between faba bean-maize and wheat-maize intercrops (P>0.10 in both cases).
Li *et al.* (2007)		Faba bean- maize cf maize-wheat	Baiyun Experimental Site, Western Gansu Province, China	Under low P_2O_5 application (0, 37.5, and 75 kg/ha) maize above-ground biomass in the faba bean-maize compared to the wheat-maize intercrop was increased by 32%, 55% and 19% (P<0.05 in all cases), respectively. Under high P_2O_5 application (112.5 and 150 kg/ha) maize above-ground biomass did not differ between faba bean-maize and wheat-maize intercrops (P>0.10 in both cases).
Pappa *et al.* (2012)		Barley-pea and barley-clover	Edinburgh, UK	Total above-ground harvest-time biomass of barley intercropped with clover (4·56 t biomass/ha) and barley intercropped with pea (4·49 t biomass/ha) were significantly greater than monocropped barley (3·05 t biomass/ha). Grain yield of barley intercropped with clover (3·36 t grain/ha) was significantly greater than that in the other treatments (P<0·01).
Putnam *et al.* (1986)	Lithourgidis *et al.* (2011)	Corn-soybean	Massachusetts, USA	The intercrop showed increases in crude protein content of forage of 11-51% (under various intercropping patterns) compared to the corn monocrop.
Sadeghpour *et al.* (2014)		Barley (*Hordeum vulgare* L.) annual medic (*Medicago scutellata* L.), strip intercropping	Karaj, Semi-arid area, Iran	When the number of rows in a 50:50 replacement intercropping decreased from six rows of barley and six rows of medic (6B:6M; strip intercropping) to 4B:4M, 2B:2M and 1B:1M, barley forage yield increased by 9, 18 and 24%. Land Equivalent Ratio (LER) was highest (1.19) when barley was intercropped with annual medic in 1B:1M arrangement. The beneficial effect of intercropping was attributed to its effects on canopy structurei.e. creating a "wavy canopy", particularly in the 2b:2M and 1B:1M mixtures.
Sadeghpour *et al.* (2014)		Barley (*Hordeum vulgare* L.) and annual medic (*Medicago scutellata* L.), strip intercropping	Karaj, Semi-arid area, Iran	When the number of rows in a 50:50 replacement intercropping decreased from six rows of barley and six rows of medic (6B:6M) to 4B:4M, 2B:2M and 1B:1M, the highest protein yield was obtained from 1B:1M ratio. Pure stands of annual medic had the highest Crude Protein (CP) content (310.7 g kg^{-1} of DM) whereas sole cropping of barley had the highest Neutral Detergent Fiber (NDF) and Acid Detergent Fiber (ADF). When both forage yield and quality was considered, the intercropping of barley and medic with 1B:1M ratio was superior to any other ratios.
Tanwar *et al.* (2014)		Sorghum-legume intercropping	Pali-Marwar, Rajasthan, India, Arid region	Rainy season sorghum-legume intercropping had a marked residual effect on the succeeding wheat crop, with a maximum 19.1% yield increase resulting from the sorghum + *Sesbania* (green manuring) treatment. During the third crop cycle, this enabled a 25% reduction in fertilizer nitrogen addition to wheat, and significantly increased soil organic carbon status.
West & Griffith (1992)	Zhang & Li (2003)	Maize-soybean strip intercropping	Indiana, USA	In the intercrop there was a 26% increase in maize yield but 27% reduction in soybean yield of border rows.

Xia *et al.* (2013)	Canola-maize; Chickpea-maize; faba bean-maize; soybean-maize intercropping	Gansu, China	The average total grain yields and shoot P contents of maize-turnip, maize-faba bean, maize-chickpea and maize-soybean intercropping increased by 30.7%, 24.8%, 24.4%, and 25.3% and by 44.6%, 30.7%, 39.1%, and 28.6%, respectively, compared with weighted means of corresponding monocultures, and were highest at 40 kg Pha^{-1}.

References

Andow DA. 1991. Vegetational diversity and arthropod population response. *Annual Review of Entomology* **36:** 561-586.

Baumann DT, Kropff MJ, Bastiaans L. 2000. Intercropping leeks to suppress weeds. *Weed Resesarch* **40:** 359-374.

Bedoussac L, Justes E. 2010. Dynamic analysis of competition and complementarity for light and N use to understand the yield and protein content of a durum wheat-winter pea intercrop. *Plant and Soil* **330:** 37-54.

Caviglia OP, Sadras VO, Andrade FH. 2004. Intensification of agriculture in the south-eastern pampas – i. Capture and efficiency in the use of water and radiation in double-cropped wheat-soybean. *Field Crops Research* **87:** 117-129.

Chen C, Westcott M, Neill K, Wichman D, Knox M. 2004. Row configuration and nitrogen application for barley-pea intercropping in Montana. *Agronomy Journal* **96:** 1730-1738.

Chen YX, Zhang FS, Tang L, Zheng Y, Li YJ, Christie P, Li L. 2007. Wheat powdery mildew and foliar N concentrations as influenced by N fertilization and belowground interaction with intercropped faba bean. *Plant and Soil* **291:** 1-13.

Corre-Hellou G, Dibet A, Hauggaard-Nielsen H, Crozat Y, Gooding M, Ambus P, Dahlmann C, von Fragstein P, Pristeri A, Monti M, Jensen ES. 2011. The competitive ability of pea-barley intercrops against weeds and the interactions with crop productivity and soil N availability. *Field Crops Research* **122:** 264-272.

Dhima, KV, Vasilakoglou, IB, Keco, R Xh, Dima, AK, Paschalidis, KA, Gatsis, TD. 2013. Forage yield and competition indices of faba bean intercropped with oat. Grass and Forage Science **69**: 376–383.

Dordas, CA, Lithourgidis, AS. 2011. Growth, yield and nitrogen performance of faba bean intercrops with oat and triticale at varying seeding ratios. *Grass and Forage Science* **66**: 569–577.

Ehrmann J, Ritz K. 2014. Plant:soil interactions in temperate multi-cropping production systems. *Plant Soil* **376:** 1-29.

Finckh MR, Gacek ES, Goyeau H, Lannou C, Merz U, Mundt CC, Munk L, Nadziak J, Newton AC, de Vallavielle-Pope C, Wolfe, MS. 2000. Cereal variety and species mixtures in practice, with emphasis on disease resistance. *Agronomie* **20:** 813–837.

Fininsa C. 1996. Effect of intercropping bean with maize on bean common bacterial blight and rust diseases. *International Journal of Pest Management* **42:** 51-54.

Ghaffarzadeh M, Prechac FG, Cruse RM. 1994. Grain yield response of corn, soybean, and oat grown in a strip intercropping system. *American Journal of Alternative Agriculture* **9:** 71–177.

Gao Y, Duan A, Sun J, Li F, Liu Z, Liu H, Liu Z. 2009. Crop coefficient and water-use efficiency of winter wheat/spring maize strip intercropping. *Field Crops Research* **111:** 65-73.

Garrity DP, Akinnefsi FK, Alayi OC, Weldesemayat SG, Mowo JG, Kalinganire A, Larwanou M, Bayala J. 2010. Evergreen agriculture: a robust approach to sustainable food security in Africa. *Food Security* **2:** 197-214.

Ghanbari A, Dahmardeh M, Siahsar BA, Ramroudi M. 2010. Effect of maize (*Zea mays* L.)-cowpea (*Vigna unguiculata* L.) intercropping on light distribution, soil temperature and soil moisture in arid environment. *Journal of Food, Agriculture & Environment* **8:** 102 – 108.

Gliessman SR. 1983. Allelopathic interactions in crop-weed mixtures: Applications for weed management. *Journal of Chemical Ecology* **9:** 991-999.

Gunes A, Bagci EG, Inal A. 2007. Interspecific facilitative root interactions and rhizosphere effects on phosphorous and iron nutrition between mixed grown chickpea and barley. *Journal of Plant Nutrition* **30:** 1255-1469.

Hauggaard-Nielsen H, Ambus P, Jensen ES. 2001. Interspecific competition, N use and interference with weeds in pea-barley intercropping. *Field Crops Research* **70:** 101–109.

Hummel J, Dosdall LM, Clayton GW, Turkington TK, Lupwayi NZ, Harker KN, O'Donovan JT. 2009. Canola-wheat intercrops for improved agronomic performance and integrated pest management. *Agronomy Journal* **101:** 1190-1197.

Inal A, Gunes A. 2008. Interspecific root interactions and rhizosphere effects on salt ions and nutrient uptake between mixed grown peanut/maize and peanut/barley in original saline–sodic–boron toxic soil. *Journal of Plant Physiology* **165**: 490-503.

Kanwar RS, Cruse RM, Ghaffarzadeh M, Bakhsh A, Karlen DL, Bailey TB. 2005. Corn-soybean and alternative cropping systems effects on NO3-N leaching losses in subsurface drainage water. *Applied Engineering in Agriculture* **21:** 181-188.

Li C, He X, Zhu S, Zhou H, Wang Y, Li Y, Yang J, Fan J, Yang J, Wang G, Long Y, Xu J, Tang Y, Zhao G, Yang J, Liu L, Sun Y, Xie Y, Wang H, Zhu Y. 2009. Crop diversity for yield increases. *PLoS One* **4:** 10.1371/journal.pone.0008049

Li L, Li SM, Sun JH, Zhou LL, Bao XG, Zhang HG, Zhang FS. 2007. Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. *Proceedings of the National Academy of Sciences of the USA* **104:** 11192-11196.

Li L, Sun JH, Zhang FS, Li XL, Yang SC, Rengel Z. 2001. Wheat/maize or wheat/soybean strip intercropping. I. Yield advantage and interspecific interactions on nutrients. *Field Crop Research* **71:** 123–137.

Li L, Zhang FS, Li X L, Christie P, Sun JH, Yang SC, Tang C. 2002. Interspecific facilitation of nutrient uptake by intercropped maize and faba bean. *Nutrient Cycling in Agroecosystems* **65:** 61-71.

Li L, Zhang L, Zhang F. 2013. Crop mixtures and mechanisms of overyielding. In: Levin S, ed. *Encyclopedia of Biodiversity, 2nd Edition. Volume 2.* San Diego, USA: Academic Press, 382-395.

Lithourgidis AS, Dordas CA, Damalas CA, Vlachostergios DN. 2011. Annual intercrops: an alternative pathway for sustainable agriculture. *Australian Journal of Crop Science* **5:** 396-410.

Lorenz K, Lal R. 2014. Soil organic carbon sequestration in agroforestry systems. A review. *Agronomy for Sustainable Development* **34**: 443-454.

Mao LL, Zhang LZ, Li WQ, van der Werf W, Sun JH, Spiertz H, Li L. 2012. Yield advantage and water saving in maize/pea intercrop. *Field Crops Research* **138:** 11-20.

Pappa VA, Rees RM, Walker RL, Baddeley JA, Watson CA. 2011. Nitrous oxide emissions and nitrate leaching in an arable rotation resulting from the presence of an intercrop. *Agriculture, Ecosystems and Environment* **141:** 153-161.

Pappa, VA, Rees, RM, Walker, RL, Baddeley, JA, Watson, CA. 2012. Legumes intercropped with spring barley contribute to increased biomass production and carry-over effects. *Journal of Agricultural Science* **150:** 584-594.

Poggio SL. 2005. Structure of weed communities occurring in monoculture and intercropping of field pea and barley. *Agriculture, Ecosystems and Environment* **109:** 48-58.

Putnam DH, Herbert SJ, Vargas A. 1986. Intercropped cornsoybean density studies. II. yield composition and protein. *Experimental Agriculture* **22:** 373-381.

Risch SJ. 1983. Intercropping as cultural pest control: prospects and limitations. *Environmental Management* **7:** 9-14.

Sadeghpour A, Jahanzad E, Lithourgidis AS, Hashemi M, Esmaeili A, Hosseini MB, 2014. Forage yield and quality of barley-annual medic intercrops in semi-arid environments. *International Journal of Plant Production* **8**: 77-89.

Saucke H, Ackermann K. 2006. Weed suppression in mixed cropped grain peas and false flax (*Camelina sativa*). *Weed Research* **46:** 453-461.

Szumigalski A, van Acker R. 2008. Land Equivalent Ratios, light interception, and water use in annual intercrops in the presence or absence of in-crop herbicides. *Agronomy Journal* **100:** 1145-1154.

Tanwar SPS, Rao SS, Regar PL, Datt S, Praveen-Kumar, Jodha BS, Santra P, Kumar R, Ram R. 2014. Improving water and land use efficiency of fallow-wheat system in shallow Lithic Calciorthid soils of arid region: Introduction of bed planting and rainy season sorghum-legume intercropping. *Soil & Tillage Research* **138:** 44-55.

West TD, Griffith DR. 1992. Effect of strip-intercropping corn and soybean on yield and profit. *Journal of Production Agriculture* **5:** 107–110.

Xia HY, Wang ZG, Zhao JH, Sun JH, Bao XG, Christie P, Zhang FS, Li L. 2013. Contribution of interspecific interactions and phosphorus application to sustainable and productive intercropping systems. *Field Crops Research* **154**: 53-64.

Xiong HC, Kakei Y, Kobayashi T, Guo XT, Nakazono M, Takahashi H, Nakanishi H, Shen HY, Zhang FS, Nishizawa NK, Zuo YM. 2013. Molecular evidence for phytosiderophore-induced improvement of iron nutrition of peanut intercropped with maize in calcareous soil. *Plant Cell and Environment* **36**: 1888-1902.

Yang CH, Huang GB, Chai Q, Luo ZX. 2011. Water use and yield of wheat/maize intercropping under alternate irrigation in the oasis field of northwest China. *Field Crops Research* **124:** 426-432.

Zeller SL, Kalinina O, Flynn DFB, Schmid B. 2012. Mixtures of genetically modified wheat lines outperform monocultures. *Ecological Application* **22:** 1817- 1826.

Zhang F, Li L. 2003. Using competitive and facilitative interactions in intercropping systems enhances crop productivity and nutrient use efficiency. *Plant and Soil* **248:** 305-312.

Zhu YY, Chen HR, Fan JH, Wang YY, Li Y, Chen JB, Fan JX, Yang SS, Hu LP, Leung H Mew TW, Teng PS, Wang ZH, Mundt CC. 2000. Genetic diversity and disease control in rice. *Nature* **406:** 718-722.

Zougmore R, Kambou FN, Ouattara K, Guillobez S. **2000.** Sorghum-cowpea intercropping: An effective technique against runoff and soil erosion in the Sahel (Saria, Burkina Faso). *Arid Land Research and Management* **14:** 329-342.